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The Neogene tropical America fish assemblage and the paleobiogeography of the Caribbean region

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Abstract This first analysis of the marine fish fossil record in the Caribbean region during the Neogene is based on comprehensive new faunal compilation lists at the generic level from basins of nine Central and South American countries during Miocene and Pliocene times. Joint ordination and classification techniques were used to analyze data comprising 236 genera and 346 species. Principal Component Analyses were used to calculate covariance and variance between localities. We identified four subprovinces, representing four different patterns. The subprovince of Venezuela shows distinct and unique features since the Neogene in the diversity of ecosystems represented. The Antillean subprovince has a western orientation and is composed of Jamaica, the Dominican Republic, and the Trinidad islands. The third subprovince combines Panama and Ecuador. It reflects the Pacific faunal influence into the proto-Caribbean and a characteristic benthopelagic fauna. The fourth subprovince is Costarican. Its nektonic fish fauna reflects the overprinting impact over the proto-Caribbean fish fauna mostly due to local paleoenvironmental changes (neritic, estuarine and deep water assemblages), whereby the overall composition of genera is largely not affected (except few lamnids, such as the giant-toothed white sharks and the wide-toothed mako shark). The results of the analyses are concordant with previous ones based on invertebrates and identified regions in need of study (e.g., Colombia, Nicaragua, Honduras, and Brazil).

Keywords Neogene · Caribbean · Gatunian · Province · Teleostean · Elasmobranch

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Introduction

The formation of the Caribbean Sea coupled with that of the Panamanian Isthmus during the latest part of the Cenozoic Era resulted in one of the great natural experiments in evolution. The 'Great American Biotic Interchange' that took place in the continental communities has been largely addressed by studies of vertebrate animals, most specially mammals (Webb, 2006; Woodburne, 2010). Our understanding of the changes in marine environments is based on investigations of diverse invertebrate groups. Dynamic processes of the ocean currents, physical and chemical water mass conditions, and geographic configurations including Caribbean isolation along the geochronological sequence, produced direct influence over the Neogene Amphi-American marine communities (Corals: Johnson, Sánchez-Villagra, & Aguilera, 2009; Budd, Stemann, & Johnson, 1994, 1996; crustacean decapods: Schweitzer & Iturralde-Vinent, 2005; Collins, Portell, & Donovan, 2009; Aguilera, Rodrigues de Aguilera, Vega, & Sánchez-Villagra, 2010; echinoids: Mihaljević et al., 2010; mollusks: Jackson, Jung, Coates, & Collins, 1993; bryozoans: Cheetham & Jackson, 1996; Cheetham, Jackson, & Sanner,

2001; O'Dea, Herrera-Cubilla, Fortunato, & Jackson, 2004; O'Dea et al., 2007 O'Dea & Jackson, 2009). These faunal changes are characterized by extinction and turnover in Miocene–Pliocene times.

We address the paleobiogeography in this region and geological time using a rich and complex new database of fossil fish taxa, thus investigating for the first time the marine realm with the most diverse group of vertebrates. The data include almost 100 'families', 236 genera, and 346 species, from 11 Neogene basins in Tropical America. We aim to produce the first qualitative and quantitative analysis of marine fish diversity of the past Caribbean biogeography.

We adopt the term "Gatunian Province" (Landau, Vermeij, & Marques da Silva, 2008) for the geographical area (proto-Caribbean) and the geochronological sequence (Miocene–Pliocene) of interest. This region presents a rich basis for investigation considering the geographic displacement, emersions, and submersions of sedimentary basins, transgression and regression of the sea level, changes in the oceanographic conditions, and species extinction and turnover. There is an ongoing debate over the geographic extension and geochronologic subprovinces involved (Woodring, 1974; Petuch, 1982, 1988, 2004; Landini, Carnevale, & Sorbini, 2002a; Landini et al., 2002b; Porta, 2003; Landau et al., 2008; Harnik, Jablonski, Krug, & Valentine, 2010; Távora, Rodrigues dos Santos, & Neto, 2010). Multiple tectonic and geographical variables were considered in the early model of Caribbean biogeography developed by Rosen (1975) based on living fauna and considering monophyletic clades. Rosen (1975) found for example the influence of the Pacific faunas on the Caribbean and mentioned a 'track Pacific–Atlantic'. Although not comparable in extent or approach, our work on monophyletic clades of fish in geological time, represents an independent examination of a similar region to that examined by Rosen (1975).

The tectonic context

The geographic configuration of Tropical America during the Cenozoic is the result of the Caribbean plate tectonic interaction with the North American, South American, Nazca, and Cocos plates (e.g. Wadge & Bunke, 1983; Pindell & Barrett, 1990; Pindell et al., 2005; Bachmann, 2001; Iturralde-Vinent, 2004–2005). The tectonic dynamic involved the subduction of western Central America and the eastern Lesser Antilles, the displacement of the Greater and Lesser Antilles and the volcanic island arc coupled with the uplift of the Panama Isthmus (Wadge & Bunke, 1983; Coates & Obando, 1996; Hoernle et al., 2002). These events resulted in the faunal isolation of the Western Central Atlantic and the Eastern Central Pacific at about 3.5 Ma, and the displacement of the multiple sedimentary basins to different geographic locations through time. Prior to the formation of the Panamanian barrier, the trans-isthmus passage was an open seaway permitting a strong inflow of the equatorial Pacific current into the proto-Caribbean, characterized by rich nutrient concentrations to produce high primary productivity (Schneider & Schmittner, 2006; Newkirk & Martin, 2009). The superficial circumtropical current went in western direction through the Panamanian seaway, towards the Pacific Ocean (Iturralde-Vinent & MacPhee, 1999; Schweitzer, Iturralde-Vinent, Hetler, & Velez-Juarbe, 2006).

Methods

Data were obtained from sampling during field trips to Ecuador, Costa Rica, Panama, and Venezuela under the scope of the Panama Paleontology Project (PPP), with identifications and leadership in this portion of the work by the senior author and in co-operation with Werner Schwarzhans (Hamburg) in respect to joint publications in preparation. The local geology and stratigraphical reference follow Coates, Collins, Aubry, and Berggren (2004); (Coates, McNeill, Aubry, Berggren, and Collins, 2005), and Quiróz and Jaramillo (2010). The field trip to Brazil was under the scope of the Museu Emilio Goeldi Paleontology Project; the geological and stratigraphical references follow Rossetti and Góes (2004). Specimens from Trinidad and Dominican Republic were studied based on additional PPP samples and collections at the Museum of Natural History of Belgium, Museum of Natural History of Basel, and Smithsonian Natural History Museum. Data from Cuba, Puerto Rico, Grenadines, Tobago, and Jamaica as well as complementary information from the other countries were taken from published literature (Table 1). Our data were standardized at the generic level, as is common in this kind of study (Foote & Miller, 2007). This procedure served also to diminish distortions caused by preservation and sampling biases, endemic groups and nomenclatural uncertainties.

We grouped basins according to the countries studied, which are deemed good representatives of the Miocene–Pliocene sequence forming the proto-Caribbean Gatunian Province in terms of geographical, paleoenvironmental and geochronological sequence (Table 1). Biases are sometimes attributed to few samples of taxa in certain basins (e.g., Barbados Island) or the absence (lack of preservation or study) of teleosteans or elasmobranchs (e.g., Brazil and Dominican Republic, respectively).

Merging of different time periods for the analysis is justified as there is a well-defined and restricted geological time window represented by the data. Once more precise

Table 1 References of fossil fish records by authors, formations, and age for each country-basin

Country-basin	Reference	Age (formation)
Cuba	Sánchez, 1920	Eocene (Universidad and Consuelo)
	Iturralde-Vinent et al., 1996, 1998	Early Miocene (Husillo)
	Iturralde-Vinent & Case, 1998	Early to Middle Miocene (Cojimar)
	Días-Franco & Rojas-Consuegra, 2009	Middle Miocene (Guines)
		Late Miocene to Pliocene (Canímar)
Jamaica	Purdy et al., 1996	Middle Eocene (Chapelton)
	Stringer, 1998	Miocene (Montpelier)
	Donovan & Gunter, 2001	Pliocene (Bowden Shell Bed)
	Ch. Underwood & Mitchell, 2004	
Dominican	Nolf & Stringer, 1992	Late Miocene (Cercado)
Republic	Schwarzhans, 1997	Late Miocene to Early Pliocene (Gurabo)
		Early to middle Pliocene (Mao)
Puerto Rico	Nieves-Rivera, 1999	Middle Miocene (Aymamón)
	Nieves-Rivera et al., 2003	
Venezuela	Casier, 1958	Late Eocene to Early Miocene (Castillo)
	Leriche, 1938	Early Miocene (Cantaure)
	Nolf & Aguilera, 1998	Late Miocene (Socorro, Codore and Urumaco)
	Sánchez-Villagra et al., 2000	Late Miocene to Early Pliocene (Cubagua)
	Aguilera & Rodrigues de Aguilera, 2001, 2004a, b, c	Pliocene (San Gregorio, Paraguaná, Tortuga and Cumaná)
	Aguilera, 2004, 2010	
	Aguilera et al., 2008	
	Aguilera & Lunddberg, 2010	
Costa Rica	Aguilera & Rodrigues de Aguilera, 1999	Late Miocene (Río Banano, Curré and Punta Judas)
		Late Miocene to Early Pliocene (Uscari)
	Collins et al., 1999	
	Laurito, 1996, 1999, 2004	
	Laurito & Valerio, 2008	
	Laurito et al., 2008	
Panama	Blake, 1862	Early Miocene (Tuira)
	Gillette, 1984	Middle Miocene (Chucunaque and Valiente)
	Aguilera & Rodrigues de Aguilera, 1999	Middle Miocene to Late Miocene (Gatun)
		Late Miocene (Nancy Point, Chagre and Uscari)
	Collins et al., 1999	Late Miocene to Early Pliocene (Shark Hole Point)
	Pimiento et al., 2010	Pliocene (Cayo Agua and Escudo de Veraguas)
		Late Pliocene to Pleistocene (Swan Cay)
Trinidad	Nolf, 1976	Early to Middle Miocene (Brasso)
	Schwarzhans, 1993, 1997	Middle Miocene (Tamana)
		Late Miocene to Early Pliocene (Morne L'Enfer)
Tobago	Donovan et al., 2001	Pliocene (Rockly Bay formation)
Grenada	Portell et al., 2008	Early to Middle (Kendeace)
		Middle Miocene (Grand Bay)
Ecuador	Landini et al., 1991	Early Miocene (Viche)
	Landini et al., 2002a, b	Middle Miocene (Angostura)
	Bianucci et al., 1993, 1997	Pliocene (Onzole and Canoa)
		Early Pleistocene (Jama formation)
Brazil	Santos & Travassos, 1960	Early Miocene (Pirabas formation)
	Santos & Salgado, 1971	
	Malabarba, 1991	
	Reis, 2005	
	Oliveira et al., 2008	
	Ramos et al., 2009	
	Costa et al., 2004, 2009	
	Távora et al., 2010b	
	Costa, 2011	

stratigraphical and temporal information on existing, as well as on new sites becomes available, a new analysis examining changing across the time window examined will be possible.

The binary data matrix includes 236 genera of fossil fishes from nine country-basins; these were analyzed using jointly ordination and classification techniques. Initially, the classification was accomplished using a non-hierarchical K-means algorithm that gathers similar variables in a pre-established number of groups (Legendre & Legendre, 1998). Such groups are geometrically as compact as possible around their respective centroids. The method is particularly efficient when classifying widely distributed variables with many null values without the need for establishing a relative scale of dissimilarity (Legendre, Ellingsen, Bjornbom, & Casgrain, 2002). The best number of groups present in a data set was defined by maximum value of the *C–H* pseudo-*F*-statistics (Calinski & Harabasz, 1974) for different partitions (number of groups), where:

$$CH = \left[\frac{R^2}{(K-1)}\right] \cdot \left[\frac{(n-k)}{(1-R^2)}\right]$$

where,

$$R^2 = \frac{(\mathrm{SST} - \mathrm{SSE})}{\mathrm{SST}},$$

K number of groups and $n = 203$, the number of genera.

SST is the total sum of squared distances to the overall centroid and SSE is the sum of squared distances of the objects to their group's own centroids. The classification was accomplished using the free software K-MEANS2 (Legendre, 2001). In a simulation study involving many stopping rules for cluster analysis, Milligan and Cooper (1985) found that the Calinski–Harabasz criterion was the one that would best recover the correct number of groups.

The principal components analysis (PCA) uses the calculated covariance and variance between localities, for this reason this is a Q-PCA sensu Fasham (1977). The Q-PCA analysis was run using the free software PAST (Hammer, Harper, & Ryan, 2001), and the K-mean for the groups was expressed in the PCAs planes using the concentration ellipse level of 80%. Following Jackson, Somers, and Harvey (1989) the size effect of the linear relationship between the PCA axis 1 and the relative frequency of species occurrence was established with the largest occurrence.

The confidence ellipses of genera groups were formed by computing the three following procedures using PAST software (Hammer et al., 2001) as proposed by Abdi, Dunlop, & Willians (2009): (1) the coordinates of the center of the ellipse of each group in the factorial plane (Axis II and Axis III), (2) the angle between the major axis of the ellipse and the first dimension of the plane, and (3) the relative size of the minor axis compared to the major axis of the ellipse. To perform these procedures the center of the ellipse must be set at the center of mass of the points. Thereafter, the ratio between the minor axis and the major axis is calculated as done in the ratio of the second to the first eigenvalue. Finally, the angle of rotation is given by the first eigenvector. For a 70% confidence interval, the length of the axes of the ellipse is set to ensure that the ellipse comprehends 70% of the points. It is also important to note that the value of 70% was chosen for visual clarification as to avoid overlapping the ellipses.

Results and discussion

The Miocene–Pliocene fish faunal assemblage established in the Tropical American seaway before the uplift of the Panamanian isthmus is called here the proto-Caribbean fauna, because the Caribbean Sea proper was only formed after the Pacific and Atlantic isolation was complete.

In our assesment the proto-Caribbean fauna is arranged in four different paleobiogeographic patterns of countries/basins and genera assemblages following specific regional paleoenvironments. In terms of faunal composition, age and geographic distribution these four paleobiogeographic patterns can be classified as subprovinces of the Neogene Gatunian bioprovince.

The isolated vector of Venezuela (V) exhibits a pattern of co-occurrence and singularity of fossil fish genera indicated in Fig. 1a (Group 1). Fig. 1b (Group 4) shows Venezuela characterized by a larger frequency of genera of the proto-Caribbean.

Since the Neogene until today, the marine sediment basins of Venezuela represent a faunal subprovince with unique features, which distinguish it from the rest of the Caribbean in diversity of ecosystems represented (estuaries, coastal lagoons, mangrove, rocky bottom, muddy bottom, corals and sea-grasses area, sandy beaches, shallow waters and depth waters, upwelling coastal process, bays and oceanic islands). A similar conclusion was reached by Landau et al. (2008) in their revision of the paleobiogeography of the mollusks of the South Caribbean. Based on their study Landau et al. (2008) recognized a Colombia–Venezuela–Trinidad subprovince. Our analysis though shows large qualitative and quantitative differences between Venezuela and Trinidad (T). An example of the unique composition in the Venezuelan subprovince is the Lower Miocene assemblage of the Cantaure Formation (Nolf & Aguilera, 1998) and that of the Upper Miocene to Lower Pliocene Cubagua Formation (Aguilera & Rodrigues de Aguilera, 2001). The first represents a shallow water environment, and the Cubagua Formation an environment of intense coastal upwelling. The comparisons

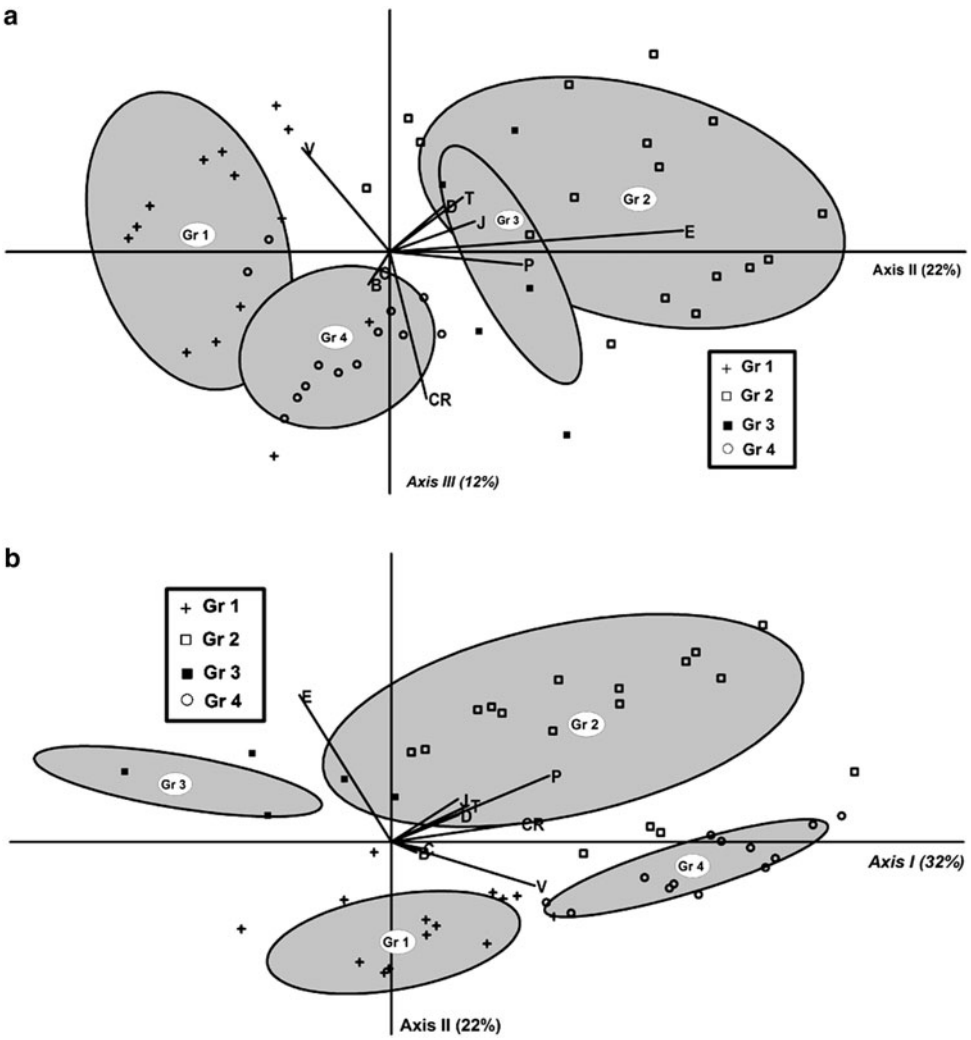

Fig. 1 Principal components analysis arranged by genera and country-basin (*B* Brazil, *C* Cuba, *CR* Costa Rica, *D* Dominican Republic, *E* Ecuador, *J* Jamaica, *P* Panamá, *T* Trinidad, *V* Venezuela), and ovoid area of fossil fish assemblage (group species 1, 2, 3 and 4). **a** Axis II versus axis III. **b** Axis I versus axis II

with Trinidad could be expanded in the future with the study of the faunas from the Springvale Formation (Landau et al., 2009). As for Colombia, the available information on Neogene fossil fish is still very preliminary and does not allow conclusions in respect to the suggestion by Landau et al. (2008).

The second subprovince identified by analysis of the fossil fish faunas is the arc of western orientated basins composed of Jamaica (J), Dominican Republic (D) and Trinidad (T) islands. Jamaica and Hispaniola (Haiti and Dominican Republic) moved eastwards along the Eastern Fault in the northern limit of the Caribbean plate during Cenozoic time (Wadge & Bunke, 1983, Pindell et al., 2005). Structural elements affecting Trinidad include a complex mix of contraction, extension, and strike-slip. In the early Cenozoic, deformation and localized uplift of some elements of the passive margin began in the Trinidad region. Through the Oligocene, the leading edge of the Caribbean plate advanced eastward imposing a transpressional deformation onto the passive margin of eastern Venezuela and Trinidad. In the late Miocene, Caribbean-South American relative motion became fundamentally translational (Lingrey, 2007). This subprovince is defined here as the Antillean subprovince and it corresponds in the analysis to the co-occurrence and the exclusivity of the group expressed in Fig. 1a (Group 3); the mean of the species frequency is expressed in Fig. 1b (Group 2).

Given that the angle resulting from the PCA is larger than 45° between Trinidad-Dominican Republic-Jamaica in relation to Panamá-Ecuador, they should best be allocated into two separate subprovinces.

The third subprovince is thus composed of Panama and Ecuador (Fig. 1a; Group 2 and overlap with Group 3). Ecuador has a singular faunal group restricted to the less genera frequency of occurrence pattern (Fig. 1b; Group 3). This pattern reflects the Pacific faunal influence into the proto-Caribbean, because Ecuador, and to some extent also Panama, show species diversity essentially typical for the East Pacific, particularly as to the benthopelagic fauna.

Previous research on Ecuador Pliocene benthonic foraminifera, mollusks, and teleostean fishes (Landini et al., 2002a, b), suggested association within a Panamanian subprovince for this region. Our results for the Miocene–Pliocene are in agreement with the proposition of Landini et al. (2002a, b), extending thus the geochronological range of the subprovince into earlier times equivalent to the proto-Caribbean.

Based on the functional structure of bryozoans and mollusks, O'Dea et al. (2006) hypothesized geochronological abiotic and biotic factors affecting the invertebrate community as consequence of the uplift of the Panamanian isthmus. The change in the water current patterns and the collapse of primary productivity did not lead to synchronous evolutionary responses with immediate extinction and turnover, but rather exhibited a time lag of 2–1 Ma. In contrast to this Pleistocene effect, Johnson et al. (2009) demonstrated that during the Oligocene–Miocene transition a major change occurred in the coral community of the proto-Caribbean with almost 50% of diversity disappearance in the lower Miocene.

The fourth subprovince is here named Costarican and is composed only of Costa Rica (CR) showing the co-occurrence pattern and the singular faunal group expressed in Fig. 1a (Group 4) characterized in the Fig. 1b by high frequency of genera occurrence in this region (Group 2). The absence of fossil fish records in adjacent Nicaragua and Honduras produces regional gaps, to be considered in future studies.

The short vectors of Brazil (B) and Cuba (C) shown by our analysis and the isolated data from Puerto Rico, Tobago, and Grenadine (Table 1) represent preliminary data. However, the associated vertebrate fauna from the lower-middle Miocene Cojimar Formation from Cuba (Iturralde-Vinent, Hubbell, & Rojas, 1996) and the lower Miocene Pirabas Formation from Brazil (Ramos, Santos, Costa, & Toledo, 2009), include similar remains of crocodiles, dugongs (Sirenia), turtles and land mammals (e.g., a rodent). Rosen (1975) had already suggested a close biogeographic link between Cuba and Brazil based on the occurrence of the swamp eel *Ophisternon*.

The fossil sharks and rays' records from Brazil, Cuba, Puerto Rico, Tobago, and Grenadine are few demersal elasmobranchs widely distributed during the Neogene.

Figure 1a shows the spatial distribution of the genera complexes in four ovoid areas that explain the 70% of the probability of occurrence. The first group is formed by 79 genera and represents the more diverse assemblage in terms of taxa and paleoenvironments (Table 2). This group is characterized mostly by the presence of shallow water demersal fishes, associated with bathypelagic and benthopelagic taxa that reflect productive and environmental stability in this zone. The second group formed by 39 genera is characterized by the presence of shallow water fishes and pelagic planktivores from the neritic zone. The third group formed by 61 genera is characterized by the presence of a large assemblage of fishes that inhabit shallow waters over mud bottom, some of them being associated with brackish environments. This group of fish is indicative for inner platform slope environments and some nocturnal migratory planktivore bathypelagic and carnivore benthopelagic taxa were present. The fourth group is composed of 20 genera, most of them shallow water sharks and rays. Large extinct lamnid sharks, medium sized hemigaleid and carcharinid sharks are present in this group, all of which were widely distributed circumtropically.

The qualitative analysis of the faunal composition based on a comprehensive species list, though preliminary in many aspects (Table 3), shows extinct genera (e.g. *Megaselachus megalodon*), extinct species (e.g. *Hemipristis serra*), and an extremely high turnover rate of species. The list of fossil fishes presented here is the most comprehensive overview and compilation of the Neogene Tropical faunal community, with shallow water (e.g. *Mugil*), brackish (e.g. *Aspistor*), demersal (e.g. *Lepophidium*), bathypelagic (e.g. *Diaphus*), benthopelagic (e.g. *Heptranchias*), and pelagic (e.g. *Mobula*) faunal elements. Benthic fish representatives exhibit preference for mud bottom (e.g. *Ariosoma*) or sandy bottom (e.g. *Stellifer*). Paleodepth indicators show a range from near shore (e.g. *Equetus*: 0–50 m) to continental slope (*Maurolichus*: 300–500 m depth), and some are known for their diurnal vertical migration (e.g. *Lampadena*).

Summary and conclusions

The fish fossil record in the proto-Caribbean presents identifiable patterns about the pre-isthmus paleobiogeography, denoting the influence of the Pacific current into the Amphi-American fish distribution in the Gatunian Province. We identified the Venezuelan, Antillean, Panamanian, and Costarican subprovinces based on a multivariate analysis of genera. These subprovinces are related to the regional geology and its tectonic dynamics coupled with the oceanographic conditions, paleodepth, and paleoenvironment.

The Caribbean geographic isolation formed as consequence of the Panamanian Isthmus and led to the Plio-Pleistocene extinction and high turnover of the species composition best documented until now in the invertebrate benthic fauna (Aguilera et al., 2010; Budd et al., 1994, 1996; Cheetham & Jackson, 1996; Cheetham et al., 2001; Collins et al., 2009; Jackson et al., 1993, 2009; Mihaljević et al., 2010; O'Dea et al., 2004, 2007; O'Dea & Jackson, 2009; Schweitzer & Iturralde-Vinent, 2005). However, the

Table 2 Functional groups (1–4) organized by genera, trophic preference and habitat

Genera	Family	Trophic	Habitat	G	ID	Genera	Family	Trophic	Habitat	G	ID
Manta	MYLIOBATIDAE	Planktivore	Pelagic	1	MANT	*Hoplostethus*	TRACHICHTHYIDAE	Carnivore	Bathypelagic	1	HOPL
Acropoma	ACROPOMATIDAE	Carnivore	Demersal	1	ACRO	*Ostichthys*	HOLOCENTRIDAE	Carnivore	Demersal	1	OSTI
Isacia	HAEMULIDAE	Carnivore	Demersal	1	ISAC	*Decapterus*	CARANGIDAE	Carnivore	Demersal	1	DECA
Diplodus	SPARIDAE	Carnivore	Demersal	1	DIPL	*Mene*	MENIDAE	Carnivore	Demersal	1	MENE
Sparus	SPARIDAE	Carnivore	Demersal	1	SPAR	*Diapterus*	GERREIDAE	Carnivore	Demersal	1	DIAP
Mokaira	ISTIOPHORIDAE	Carnivore	Pelagic	1	MAKA	*Gerres*	GERREIDAE	Carnivore	Demersal	1	GERR
Ginglymostomus	GINGLYMOSTOMATIDAE	Carnivore	Demersal	1	GING	*Haemulopsis*	HAEMULIDAE	Carnivore	Demersal	1	HAML
Antennarius	ANTENNARIDAE	Carnivore	Demersal	1	ANTE	*Aplodinotus*	SCIAENIDAE	Carnivore	Demersal	1	APLO
Lobotes	LOBOTIDAE	Carnivore	Demersal	1	LOBO	*Pachyurus*	SCIAENIDAE	Carnivore	Demersal	1	PACK
Sphyraena	SPHYRAENIDAE	Carnivore	Demersal	1	SPHA	*Bembrops*	PERCOPHIDAE	Carnivore	Demersal	1	BEMB
Notorhynchus	HEXANCHIDAE	Carnivore	Bathydemersal	1	NOTO	*Lepidopus*	TRICHIURIDAE	Carnivore	Demersal	1	LEPI
Pseudocarcharias	PSEUDOCARCHARIIDAE	Carnivore	Demersal	1	PSEU	*Achiurus*	ACHIRIDAE	Carnivore	Demersal	1	ACHI
Paratodus	LAMNIDAE	Carnivore	Pelagic	1	PARA	*Diodon*	DIODONTIDAE	Carnivore	Demersal	1	DIOD
Galeorhinus	GALEORHINIDAE	Carnivore	Benthopelagic	1	GALE	*Heptranchias*	HEXANCHIDAE	Carnivore	Benthopelagic	1	HEPT
Etmopterus	DALATIIDAE	Carnivore	Bathypelagic	1	ETMO	*Odontaspis*	ODONTASPIDIDAE	Carnivore	Demersal	1	ODON
Trigonognathus	DALATIIDAE	Carnivore	Bathydemersal	1	TRIG	*Alopias*	ALOPIIDAE	Carnivore	Benthopelagic	1	ALOP
Dalatias	DALATIIDAE	Carnivore	Bathydemersal	1	DALA	*Mustelus*	TRIAKIDAE	Carnivore	Benthopelagic	1	MUST
Centrophorus	CENTROPHORIDAE	Carnivore	Bathydemersal	1	CENT	*Isogomphodon*	CARCHARHINIDAE	Carnivore	Demersal	1	ISOG
Daenia	CENTROPHORIDAE	Carnivore	Bathydemersal	1	DAEN	*Squalus*	SQUALIDAE	Carnivore	Bathypelagic	1	SQUA
Pristiophorus	PRISTIOPHORIDAE	Carnivore	Demersal	1	PRIS	*Squatina*	SQUATINIDAE	Carnivore	Benthopelagic	1	SQAT
Pteromylaeus	MYLIOBATIDAE	Carnivore	Benthopelagic	1	PTER	*Raja*	RAJIDAE	Carnivore	Benthopelagic	1	RAJA
Plinthicus	MYLIOBATIDAE	Carnivore	Benthopelagic	1	PLIN	*Rhinchobatos*	RHINOBATIDAE	Carnivore	Demersal	1	RHIB
Japonoconger	CONGRIDAE	Carnivore	Demersal	1	JAPO	*Mobula*	MYLIOBATIDAE	Planktivore	Plagic	1	MOBU
Conger	CONGRIDAE	Carnivore	Demersal	1	CONG	*Steindachneria*	MERLUCCIDAE	Carnivore	Benthopelagic	1	STEI
Cynoponthicus	MURAENESOCIDAE	Carnivore	Demersal	1	CYNP	*Odontaspis*	ODONTASPIDIDAE	Carnivore	Demersal	1	ODON
Harengula	CLUPEIDAE	Planktivore	Pelagic	1	HARE	*Ophioscion*	SCIAENIDAE	Carnivore	Demersal	1	OPHS
Amphiarius	ARIIDAE	Carnivore	Demersal	1	AMPH	*Carcharias*	ODONTASPIDIDAE	Carnivore	Demersal	1	EUGO
Aspistor	ARIIDAE	Carnivore	Demersal	1	ASPI	*Narcine*	NARCINIDAE	Carnivore	Demersal	1	NARC
Notarius	ARIIDAE	Carnivore	Demersal	1	NOTA	*Rhinoptera*	MYLIOBATIDAE	Carnivore	Demersal	1	RHIT
Bagre	ARIIDAE	Carnivore	Demersal	1	BAGR	*Sciades*	ARIIDAE	Carnivore	Demersal	1	SCIA
Argentina	ARGENTINIDAE	Carnivore	Demersal	1	ARGE	*Symbolophorus*	MYCTOPHIDAE	Planktivore	Bathypelagic	1	SYMB
Scopelosaurus	NOTOSUDIDAE	Planktivore	Bathypelagic	1	SCOP	*Polymixia*	POLYMIXIIDAE	Carnivore	Bathydemersal	1	POLX
Neoscopelus	NEOSCOPELIDAE	Planktivore	Bathypelagic	1	NEOS	*Thalassophryne*	BATRACHOIDIDAE	Carnivore	Demersal	1	THAL
Electrona	MYCTOPHIDAE	Planktivore	Bathypelagic	1	ELEC	*Ocyurus*	LUTJANIDAE	Carnivore	Demersal	1	OCYU
Physiculus	MORIDAE	Carnivore	Demersal	1	PHYS	*Plagioscion*	SCIAENIDAE	Carnivore	Demersal	1	PLAG
Snyderidia	CARAPIDAE	Carnivore	Demersal	1	SYND	*Protosciaena*	SCIAENIDAE	Carnivore	Demersal	1	PROT
Membras	ATHERINIDAE	Carnivore	Demersal	1	MEMB	*Albula*	ALBULIDAE	Carnivore	Demersal	1	ALBU

Table 2 continued

Genera	Family	Trophic	Habitat	G	ID	Genera	Family	Trophic	Habitat	G	ID
Melamphaes	MELAMPHAIDAE	Planktivore	Bathypelagic	1	MELA	*Myctophum*	MYCTOPHIDAE	Planktivore	Bathypelagic	1	MYCT
Hyporhamphus	HEMIRHAMPHIDAE	Carnivore	Demersal	1	HYPO	*Diaphus*	MYCTOPHIDAE	Planktivore	Bathypelagic	2	DIAP
Hildebrandia	CONGRIDAE	Carnivore	Demersal	1	HILDE	*Bregmaceros*	BREGMACEROTIDAE	Carnivore	Demersal	2	BREG
Epigonus	EPIGONIDAE	Carnivore	Bathydemersal	1	EPIG	*Porichthys*	BATRACHOIDIDAE	Carnivore	Demersal	2	PORI
Engraulis	ENGRAULIDAE	Planktivore	Pelagic	2	ENGR	*Apogon*	APOGONIDAE	Carnivore	Demersal	2	APOG
Maurolicus	STERNOPTYCHIDAE	Planktivore	Bathypelagic	2	MAUR	*Ariosoma*	CONGRIDAE	Carnivore	Demersal	2	ARIO
Saurida	SYNODONTIDAE	Carnivore	Demersal	2	SAUR	*Gnathophis*	CONGRIDAE	Carnivore	Demersal	3	GNAT
Coelorhinchus	MACROURIDAE	Carnivore	Benthopelagic	2	COEL	*Clupea*	CLUPEIDAE	Planktivore	Pelagic	3	CLUP
Ophidion	OPHIDIIDAE	Carnivore	Demersal	2	OPHI	*Eutrumeus*	CLUPEIDAE	Planktivore	Pelagic	3	EURU
Cetengraulis	ENGRAULIDAE	Planktivore	Pelagic	2	CENT	*Anchovia*	ENGRAULIDAE	Planktivore	Pelagic	3	ANCV
Trachurus	CARANGIDAE	Carnivore	Demersal	2	TRAC	*Yarella*	NEOSCOPELIDAE	Planktivore	Bathypelagic	3	YARE
Cynoscion	SCIAENIDAE	Carnivore	Demersal	2	CYNO	*Ceratoscopelus*	MYCTOPHIDAE	Planktivore	Bathypelagic	3	CERA
Equetus	SCIAENIDAE	Carnivore	Demersal	2	EQUE	*Lampadena*	MYCTOPHIDAE	Planktivore	Bathypelagic	3	LAMP
Larimus	SCIAENIDAE	Carnivore	Demersal	2	LARM	*Steindachneria*	MERLUCCIIDAE	Carnivore	Bathypelagic	3	STEN
Paralonchurus	SCIAENIDAE	Carnivore	Demersal	2	PARL	*Notoscopelus*	MYCTOPHIDAE	Planktivore	Bathypelagic	3	NOTO
Syacium	PARALICHTHYIDAE	Carnivore	Demersal	2	SYAC	*Paragadus*	OPHIDIIDAE	Carnivore	Bathydemersal	3	PARG
Hygophum	MYCTOPHIDAE	Planktivore	Bathypelagic	2	HYGO	*Hoplobrotula*	OPHIDIIDAE	Carnivore	Benthopelagic	3	HOPL
Otophidium	OPHIDIIDAE	Carnivore	Demersal	2	OTOP	*Genypterus*	OPHIDIIDAE	Carnivore	Bathydemersal	3	GENY
Echiodon	CARAPIDAE	Carnivore	Demersal	2	ECHI	*Cataetyx*	BYTHITIDAE	Carnivore	Benthopelagic	3	CATA
Opisthonema	CLUPEIDAE	Planktivore	Pelagic	2	OPIS	*Carapus*	CARAPIDAE	Carnivore	Demersal	3	CARA
Umbrina	SCIAENIDAE	Carnivore	Demersal	2	UMBR	*Antennarius*	ANTENNARIDAE	Carnivore	Demersal	3	ANTE
Pythomichthys	HETERENCHELIDAE	Carnivore	Demersal	2	PYTH	*Paralabrax*	SERRANIDAE	Carnivore	Demersal	3	PARX
Opisthonema	CLUPEIDAE	Planktivore	Pelagic	2	OPIS	*Prionodes*	SERRANIDAE	Carnivore	Demersal	3	PRIO
Anchoa	ENGRAULIDAE	Planktivore	Pelagic	2	ANCH	*Pseudochromis*	PSEUDOCHROMIDAE	Carnivore	Demersal	3	PSEU
Arius	ARIIDAE	Carnivore	Demersal	2	ARIU	*Anisostrema*	HAEMULIDAE	Carnivore	Demersal	3	ANIS
Plotosus	PLOTOSIDAE	Carnivore	Demersal	2	PLOT	*Brachydeuteres*	HAEMULIDAE	Carnivore	Demersal	3	BRAC
Myripristis	HOLOCENTRIDAE	Carnivore	Demersal	2	MYRI	*Nemipterus*	NEMIPTERIDAE	Carnivore	Demersal	3	NEMI
Citharichthys	PARALICHTHYIDAE	Carnivore	Demersal	2	CITH	*Genyonemus*	SCIAENIDAE	Carnivore	Demersal	3	GENY
Symphurus	CYNOGLOSSIDAE	Carnivore	Demersal	2	SYMP	*Isopisthus*	SCIAENIDAE	Carnivore	Demersal	3	ISOP
Paraconger	CONGRIDAE	Carnivore	Demersal	2	PCON	*Menticirrhus*	SCIAENIDAE	Carnivore	Demersal	3	MENT
Lepophidium	OPHIDIIDAE	Carnivore	Demersal	2	LEPO	*Pareques*	SCIAENIDAE	Carnivore	Demersal	3	PARQ
Eucinostomus	GERREIDAE	Carnivore	Demersal	2	EUCI	*Seriphus*	SCIAENIDAE	Carnivore	Demersal	3	SERI
Lactarius	LACTARIIDAE	Carnivore	Bathydemersal	2	LACT	*Stellifer*	SCIAENIDAE	Carnivore	Demersal	3	STEL
Mugil	MUGILIDAE	Carnivore	Demersal	2	MUGI	*Strongylurus*	BELONIDAE	Carnivore	Demersal	3	STRO
"Gobiidarum"	GOBIIDAE	Carnivore	Demersal	2	GOBI	*Hemirhamphus*	HEMIRHAMPHIDAE	Carnivore	Demersal	3	HEMR
Lonchopisthus	OPISTOGNATHIDAE	Carnivore	Demersal	2	LONC	*Euleptorhamphus*	HEMIRHAMPHIDAE	Carnivore	Demersal	3	EULE
Pristipomoides	LUTJANIDAE	Carnivore	Demersal	2	PRTO	*Cymatogaster*	EMBIOTOCIDAE	Carnivore	Demersal	3	CYMA

Table 2 continued

Genera	Family	Trophic	Habitat	G	ID	Genera	Family	Trophic	Habitat	G	ID
Haemulon	HAEMULIDAE	Carnivore	Demersal	2	HAEM	*Hyperprosopon*	EMBIOTOCIDAE	Carnivore	Demersal	3	HYPE
Micrometrus	EMBIOTOCIDAE	Carnivore	Demersal	3	MICE	*Pristis*	PRISTIDAE	Carnivore	Demersal	4	PRST
Abudefduf	POMACENTRIDAE	Carnivore	Demersal	3	ABUD	*Rhynchobatus*	RHINOBATIDAE	Carnivore	Demersal	4	RHYN
Chromis	POMACENTRIDAE	Carnivore	Demersal	3	CROM	*Isurus*	LAMNIDAE	Carnivore	Demersal	4	ISUR
"Labridarum"	LABRIDAE	Carnivore	Demersal	3	LABR	*Aetobatus*	MYLIOBATIDAE	Carnivore	Demersal	4	AETO
"Dactyloscopidarum"	DACTYLOSCOPIDAE	Carnivore	Demersal	3	DACT	*Myliobatis*	MYLIOBATIDAE	Carnivore	Demersal	4	MYLI
Eopseptta	PLEURONECTHYDAE	Carnivore	Demersal	3	EOPS	*Gadella*	MORIDAE	Carnivore	Benthopelagic	4	GADL
Isopsetta	PLEURONECTHYDAE	Carnivore	Demersal	3	ISOP	*Neobythites*	OPHIDIIDAE	Carnivore	Demersal	4	NEOB
"Soleidarum"	SOLEIDAE	Carnivore	Demersal	3	SOLE	*Parascombrops*	ACROPOMATIDAE	Carnivore	Demersal	4	PRAS
Laemonema	MORIDAE	Carnivore	Benthopelagic	3	LAEM	*Galeocerdo*	CARCHARHINIDAE	Carnivore	Demersal	4	GALO
Rhechias	CONGRIDAE	Carnivore	Demersal	3	RHEC	*Sphyrna*	SPHYRNIDAE	Carnivore	Demersal	4	SPHY
Rhynchobatus	RHINOBATIDAE	Carnivore	Demersal	3	RHYN	*Megaselachus*	OTODONTIDAE	Carnivore	Demersal	4	MEGA
Neoopisthopterus	PRISTIGASTERIDAE	Planktivore	Pelagic	3	NEOP	*Carcharhinus*	CARCHARHINIDAE	Carnivore	Demersal	4	CARC
Pellona	CLUPEIDAE	Planktivore	Pelagic	3	PELL	*Sphyraena*	SPHYRAENIDAE	Carnivore	Demersal	4	SPHA
Ctengraulis	ENGRAULIDAE	Planktivore	Pelagic	3	CETN	*Hemipristis*	HEMIGALEIDAE	Carnivore	Demersal	4	HEMI
Lampanictus	MYCTOPHIDAE	Planktivore	Bathypelagic	3	LAMI	*Dasyatis*	DASYATIDAE	Carnivore	Demersal	4	DASY
Merluccius	MERLUCCIIDAE	Carnivore	Demersal	3	MERL	*Trichiurus*	TRICHIURIDAE	Carnivore	Demersal	4	TRIC
Brotula	OPHIDIIDAE	Carnivore	Benthopelagic	3	BROT						
Prionotus	TRIGLIDAE	Carnivore	Demersal	3	PRIO						
Epinephelus	SERRANIDAE	Carnivore	Demersal	3	EPIN						
Lutjanus	LUTJANIDAE	Carnivore	Demersal	3	LUTJ						
Orthopristis	HAEMULIDAE	Carnivore	Demersal	3	ORTH						
Pomadasys	HAEMULIDAE	Carnivore	Demersal	3	POMA						
Micropogonias	SCIAENIDAE	Carnivore	Demersal	3	MICR						
Sciaena	SCIAENIDAE	Carnivore	Demersal	3	SCIA						
Sciaenops	SCIAENIDAE	Carnivore	Demersal	3	SCOP						
Peprilus	STROMATIDAE	Carnivore	Demersal	3	PEPR						
Bairdiella	SCIAENIDAE	Carnivore	Demersal	3	BAIR						
Ilisha	PRISTIGASTERIDAE	Planktivore	Pelagic	3	ILIS						
Cetengraulis	ENGRAULIDAE	Planktivore	Pelagic	3	CTEN						
Nebrius	GINGLYMOSTOMATIDAE	Carnivore	Demersal	3	NEBR						
Heterodontus	HETERODONTIDAE	Carnivore	Demersal	4	HETE						
Nebrius	GINGLYMOSTOMATIDAE	Carnivore	Demersal	4	NEBR						
Negaprion	CARCHARHINIDAE	Carnivore	Demersal	4	NEGA						
Rhyzoprionodon	CARCHARHINIDAE	Carnivore	Demersal	4	RHIZ						
Isistius	DALATIIDAE	Carnivore	Benthopelagic	4	ISIS						

Table 3 Fossil marine fish species occurrence by country-basin

Order	Family	Species	Venezuela	Panama	Costa Rica	Dominican Republic	Cuba	Trinidad	Puerto Rico	Jamaica	Barbados	Ecuador	Brazil	ID
ELASMOBRANCHII														
Hexanchiformes	Hexanchidae	*Heptranchias perlo*	x		x									HEPT
		Heptranchias tenuidens	x											HEPT
		Notorhynchus sp.	x											NOTO
	Chlamydoselachidae	*Chlamydoselachus* sp.										x		CHLA
Heterodontiformes	Heterodontidae	*Heterodontus* sp.	x	x	x									HETE
Orectolobiformes	Ginglymostomatidae	*Ginglymostoma delfortriei*	x	x	x									GING
		Ginglymostoma sp.											x	GING
		Nebrius obliquus										x	x	NEBR
Lamniformes	Odontaspididae	*Carcharias taurus*	x				x							CRIA
		Odontaspis ferox	x											ODON
		Odontaspis sp.		x										ODON
	Pseudocarchariidae	*Pseudocarcharias kamoharai*	x											PSEU
	Otodontidae	*Megaselachus megalodon*	x	x	x	x	x		x					MEGA
		Megaselachus subauriculatus	x				x						x	MEGA
	Lamnidae	*Cosmopolitodus hastalis*	x											COSM
		Isurus cf. *oxyrinchus*			x									ISUR
		Isurus sp.		x	x								x	ISUR
		cf. Paratodus sp.	x											PARA
	Alopiidae	*Alopias superciliosus*	x		x						x			ALOP
		Alopias vulpinus	x											ALOP
		Alopias sp.										x		ALOP
Carcharhiniformes	Triakidae	*Mustelus* sp.	x		x									MUST
		Galeorhinus sp.	x											GALE
	Hemigaleidae	*Hemipristis serra*	x	x	x		x	x		x	x		x	HEMI
	Carcharhinidae	*Carcharhinus albimarginatus*			x									CARC
		Carcharhinus egertoni	x	x				x						CARC
		Carcharhinus falciformes	x		x									CARC
		Carcharhinus limbatus	x											CARC
		Carcharhinus longimanus			x									CARC
		Carcharhinus macloti											x	CARC
		Carcharhinus cf. *obscurus*	x				x							CARC
		Carcharhinus cf. *perezi*	x				x							CARC
		Carcharhinus plumbeus	x											CARC
		Carcharhinus priscus			x								x	CARC

Table 3 continued

Order	Family	Species	Venezuela	Panama	Costa Rica	Dominican Republic	Cuba	Trinidad	Puerto Rico	Jamaica	Barbados	Ecuador	Brazil	ID
		Carcharhinus vonderschimitti	x											CARC
		Carcharhinus sp.	x	x				x		x		x	x	CARC
		Galeocerdo aduncus	x		x		x	x						GALO
		Galeocerdo cuvier	x	x										GALO
		Galeocerdo sp.							x					GALO
		Isogomphodon acuarius			x									ISOG
		Isogomphodon caunellensis			x									ISOG
		Isogomphodon sp.	x		x									ISOG
		Negaprion eurybathrodon	x	x			x					x		NEGA
		Rhizoprionodon taxandriae	x		x									SCOL
		Rhizoprionodon sp.	x	x	x							x		RHIZ
	Sphyrnidae	*Sphyrna arambourgi*			x									SPHY
		Sphyrna cf. *lewini*							x					SPHY
		Sphyrna cf. *media*											x	SPHY
		Sphyrna zygaena			x									SPHY
		Sphyrna sp.	x	x	x		x					x		SPHY
Squaliformes	Dalatiidae	*Dalatias* sp.	x											DALA
		Isistius aff. *triangulus*	x	x	x							x		ISIS
	Etmopteridae	*Etmopterus* sp.	x											ETMO
		Trigonognathus aff. *kabeyai*	x											TRIG
	Centrophoridae	*Centrophorus* sp.	x											CENT
		Deania sp.	x							x				DEAN
	Squalidae	*Scymnodon* aff. *obscurus*								x				SCYM
		Squalus stehlini	x											SQUA
		Squalus sp.	x		x							x		SQUA
		Squaliolus schaubi								x				SQLI
Pristiophoriformes	Pristiophoridae	*Pristiophorus* sp.	x									x		PRIS
Squatiniformes	Squatinidae	*Squatina dumerili*	x		x									SQAT
		Squatina sp.										x		SQAT
Pristiformes	Pristidae	*Pristis pectinata*	x											PRST
		Pristis sp.	x	x	x									PRST
Torpediniformes	Narcinidae	*Narcine* sp.	x											NARC
Rajiformes	Rhinobatidae	*Rhinobatos* sp.	x										x	RHIB
		Rhynchobatus sp.	x	x	x									RHYN
	Rajidae	*Raja* sp.	x		x									RAJA

Table 3 continued

Order	Family	Species	Venezuela	Panama	Costa Rica	Dominican Republic	Cuba	Trinidad	Puerto Rico	Jamaica	Barbados	Ecuador	Brazil	ID
Myliobatiformes	Dasyatidae	*Dasyatis cavernosa*			x									DASY
		Dasyatis sp.	x	x	x							x	x	DASY
	Myliobatidae	*Aetobatus arcuatus*	x	x	x		x					x	x	AETO
		Manta sp.		x										MANT
		Mobula sp.	x		x									MOBU
		Myliobatis sp.	x	x			x					x	x	MYLI
		Plinthicus stenodon	x						x			x		PLIN
		Pteromylaeus sp.	x											PTER
		Rhinoptera sp.	x		x							x		RHIT
TELEOSTEI														
Albuliformes	Albulidae	*Albula* sp.	x		x	x								ALBU
Anguilliformes	Congridae	*Ariosoma balearicum*	x	x	x	x		x		x				ARIO
		Ariosoma selenops	x			x								ARIO
		Ariosoma sp.			x			x				x		ARIO
		Conger sp.	x											CONG
		Gnathophis sp.										x		GNAT
		Hildebrandia flava	x			x		x						HILD
		Hildebrandia gracilior	x											HILD
		Japanoconger caribeus	x											JAPA
		Paraconger guianensis	x	x	x					x		x		PCON
		Paraconger californiensis										x		PCON
		Rhechias sp.			x			x				x		RHEC
		Rhynchoconger cf. *nitens*										x		RHYG
		Rhynchoconger sp.			x			x				x		RHYG
	Ophichthidae	*Ophichthus* sp.		x										OPHI
	Muraenesocidae	*Cynoponthicus savanna*	x											CYNP
	Heterenchelyidae	*Pythomichthys* sp.	x	x		x		x				x		PYTH
Clupeiformes	Pristigasteridae	*Ilisha* sp.	x					x				x		ILIS
		Neoopisthopterus sp.	x									x		NEOP
	Clupeidae	*Clupea* cf. *pallasi*										x		CLUP
		Eutrumeus teres										x		EURU
		Harengula aff. *clupeola*	x	x										HARE
		Pellona sp.	x									x		PELL
		Opisthonema aff. *oglinum*	x			x		x						OPIS
		Opisthonema libertate										x		OPIS

Table 3 continued

Order	Family	Species	Venezuela	Panama	Costa Rica	Dominican Republic	Cuba	Trinidad	Puerto Rico	Jamaica	Barbados	Ecuador	Brazil	ID
	Engraulidae	*Anchoa* cf. *compressa*										x		ANCH
		Anchoa cf. *nasos*										x		ANCH
		Anchoa sp.	x	x				x				x		ANCH
		Anchovia macrolepidota										x		ANCV
		Cetengraulis mysticetus						x				x		CETN
		Centengraulis sp.	x	x										CETN
		Engraulis sp.	x	x								x		ENGR
		Engraulis cf. *mordax*										x		ENGR
Siluriformes	Ariidae	*Amphiarius rugispinis*	x											AMPH
		"Arius" spp.	x	x	x	x		x				x	x	ARIU
		Aspistor cf. *luniscutis*	x											ASPI
		Aspistor cf. *quadriscutis*	x											ASPI
		Bagre bagre	x											BAGR
		Cathorops sp.	x					x						CATH
		Genidens sp.		x								x		GENI
		Notarius kessleri	x											NOTA
		Notarius troscheli	x											NOTA
		Sciades couma	x											SIAD
		Sciades dowii	x											SIAD
		Sciades sp.	x					x						SIAD
	Plotosidae	*Plotosus* sp.	x	x		x				x				PLOT
Osmeriformes	Argentinidae	*Argentina striata*	x											ARGE
Stomiiformes	Sternoptychidae	*Maurolicus muelleri*	x	x								x		MAUR
		Polyipnus sp.	x	x		x		x						POLY
Aulopiformes	Chlorophthalmidae	*Chlorophthalmus agassizi*	x											CHLO
	Notosudidae	*Scopelosaurus* sp.	x											SCOP
	Synodontidae	*Saurida brasiliensis*	x	x				x		x				SAUR
		Synodus sp.		x										SYNO
Stomiformes	Phosichthidae	*Yarella* sp.										x		YARE
		Vinciguerria sp.		x										VINC
Myctophiformes	Neoscopelidae	*Neoscopelus* sp.	x											NEOS
		cf. *Neoscopelus*	x											NEOS
	Myctophidae	*Diaphus* aff. *dumerili*	x					x						DIAP
		Diaphus aff. *problematicus*	x									x		DIAP
		Diaphus aff. *regani*	x											DIAP

Table 3 continued

Order	Family	Species	Venezuela	Panama	Costa Rica	Dominican Republic	Cuba	Trinidad	Puerto Rico	Jamaica	Barbados	Ecuador	Brazil	ID
		Diaphus aff. *splendidus*	x									x		DIAP
		Diaphus theta										x		DIAP
		Diaphus spp.	x	x	x	x		x		x		x		DIAP
		Ceratoscopelus townsendi										x		CERA
		Electrona risso	x											ELEC
		Hygophum hygomii	x	x						x		x		HYGO
		Hygophum macrochir	x	x										HYGO
		Hygophum reinhardtii										x		HYGO
		Hygophum sp.										x		HYGO
		Lampadena sp.										x		LAMP
		Lampadena jacksoni	x	x										LAMP
		Lampanyctus cupriarius	x	x										LAMI
		Lampanyctus aff. latesulcatus	x											LAMI
		Lampanyctus sp.										x		LAMI
		Lombachia sp.		x										LOMB
		Myctophum cf. *punctatum*	x			x				x				MYCT
		Myctophum sp.		x										MYCT
		Notoscopelus sp.										x		NOTO
		Symbolophorus sp.	x	x						x				SYMB
		Stenobranchius sp.										x		STEN
		Triphoturus sp.		x										TRIP
Polymixiiformes	Polymixiidae	*Polymixia* sp.	x			x								POLX
Gadiformes	Bregmacerotidae	*Bregmaceros* sp.	x	x	x	x		x		x		x		BREG
	Macrouridae	*Coelorhinchus* aff. *coelorhinchus*	x	x								x		COEL
		Nezumia sp.	x											NEZU
	Moridae	*Gadella* sp.	x	x	x			x						GADL
		Laemonema sp.				x								LAEM
		Physiculus sp.	x											PHYS
	Merlucciidae	*Merluccius* sp.	x									x		MERL
		Merluccius productus										x		MERL
		Steindachneria cf. *argentea*	x	x										STEI
Ophidiiformes	Ophidiidae	*Brotula* cf. *clarkae*										x		BROT
		Brotula sp.			x			x						BROT
		Dicrolene sp.		x										DICR

Table 3 continued

Order	Family	Species	Venezuela	Panama	Costa Rica	Dominican Republic	Cuba	Trinidad	Puerto Rico	Jamaica	Barbados	Ecuador	Brazil	ID
		cf. Genypterus sp.										x		GENY
		Hoplobrotula sp.										x		HOPL
		Lampogramnus sp.						x						LAMP
		Lepophidium aff. *aporrohox*	x											LEPO
		Lepophidium cf. *cervinum*											x	LEPO
		Lepophidium microlepis											x	LEPO
		Lepophidium sp.	x	x	x			x		x			x	LEPO
		Neobythites aff. *unicolor*	x											NEOB
		Neobythites sp.		x	x			x						NEOB
		Ophidion sp.		x									x	OPHI
		Ophidion aff. *holbrooki*	x											OPHI
		Otophidium sp.										x		OTOP
		Otophidium robinsi	x	x						x				OTOP
		Paragadus sp.										x		PARG
		Parophidion cf. *schmidti*				x								PARO
	Bythitidae	*Cataetyx* sp.										x		CATA
		"Dinematichthyinorum" smithvanizi				x								DINE
		"Dinematichthyinorum" sauli				x								DINE
	Carapidae	*Echiodon* sp.	x	x						x		x		ECHI
		Carapus sp.											x	CARA
		Snyderidia canina	x											SYND
Batrachoidiformes	Batrachoididae	*Perulibatrachus* sp.						x						PERU
		Porichthys sp.	x	x	x	x		x		x		x		PORI
		Thalassophryne sp.	x					x						THAL
Lophiiformes	Chaunacidae	*Chaunax* sp.				x								CHAU
	Antennariidae	*Antennarius* sp.						x				x		ANTE
Atheriniformes	Atherinidae	*Atherinops* sp.										x		ATHE
		Atherinomorus stipes				x								ATHM
		Membras sp.	x											MEMB
Stephanoberyciformes	Melamphaidae	*Melamphaes polylepis*	x											MELA
		Scopelogadus sp.	x											SCOP
Beryciformes	Trachichthyidae	*Hoplostethus mediterraneus*	x											HOPL
	Holocentridae	*Holocentrus* sp.				x								HOLO

Table 3 continued

Order	Family	Species	Venezuela	Panama	Costa Rica	Dominican Republic	Cuba	Trinidad	Puerto Rico	Jamaica	Barbados	Ecuador	Brazil	ID
		Myripristis sp.	x	x				x				x		MYRI
		Ostichthys sp.	x											OSTI
Scorpaeniformes	Scorpaenidae	gen., sp. ind.				x								SCOR
	Triglidae	*Prionotus* sp.	x	x										PRIO
		Prionotus cf. *stephanophris*										x		PRIO
Perciformes	Centropomidae	*Centropomus* aff. *pectinatus*	x											CENT
		Centropomus aff. *undecimalis*	x	x		x								CENT
		Centropomus sp.										x		CENT
	Acropomatidae	*Acropoma* sp.			x									ACRO
		Parascombrops aff. *argyreus*	x	x	x					x				PRAS
	Serranidae	*Centropristls* sp.				x								CENP
		Epinephelus itajara	x											EPIN
		Epinephelus sp.										x		EPIN
		aff. *Neanthias* sp.						x						NEAN
		Paralabrax sp.										x		PARX
		Prionodes sp.										x		PRIO
		Serranus sp.		x										SERR
	Pseudochromidae	*Pseudochromis* sp.										x		PSEU
	Bathyclupeidae	*Bathyclupea* sp.						x						BATH
	Opistognathidae	*Lonchopisthus* aff. *lemur*	x	x	x			x		x		x		LONC
		Opistognathus sp.	x	x	x							x		OPIS
	Priacanthidae	*Pristigenys* sp.				x								PRIG
	Apogonidae	*Apogon* spp.	x	x	x	x		x		x		x		APOG
	Epigonidae	*Epigonus denticulatus*	x											EPIG
		Epigonus sp.	x	x		x		x						EPIG
	Lactariidae	*Lactarius* aff. *atlanticus*	x	x	x	x								LACT
		Lactarius sp.										x		LACT
	Carangidae	*Decapterus* sp.	x											DECA
		Trachurus sp.	x	x								x		TRAC
		gen., sp. ind.						x						CARA
	Menidae	*Mene* sp.	x											MENE
	Lutjanidae	*Lutjanus* sp.	x									x		LUTJ
		Ocyurus sp.	x			x								OCYU
		Pristipomoides sp.	x	x	x	x				x		x		PRTO

Table 3 continued

Order	Family	Species	Venezuela	Panama	Costa Rica	Dominican Republic	Cuba	Trinidad	Puerto Rico	Jamaica	Barbados	Ecuador	Brazil	ID
		Rhomboplites sp.		x										RHOM
	Lobotidae	*cf. Lobotes* sp.										x		LOBO
	Gerreidae	*Diapterus* sp.	x											DIAT
		Eucinostomus sp.	x	x	x					x		x		EUCI
		Gerres sp.	x											GERR
		Moharra sp.		x										MOHA
	Haemulidae	*Anisotremus* sp.										x		ANIS
		Brachydeuteres sp.										x		BRAC
		Conodon aoreaaxi				x								CONO
		Haemulon aff. *aurolineatum*	x											HAEM
		Haemulon sp.	x	x	x	x		x		x				HAEM
		Haemulopsis sp.	x											HAML
		gen., sp. ind.										x		HRUM
		Isacia sp.			x									ISAC
		Orthopristis sp.										x		ORTH
		Orthopristis aff. *ruber*	x											ORTH
		Pomadasys aff. *panamensis*	x									x		POMA
		Pomadasys sp.						x						POMA
	Nemipteridae	*Nemipterus* sp.										x		NEMI
	Sciaenidae	*Aplodinotus hofmani*	x											APLO
		Aplodinotus longecaudatus	x											APLO
		Bairdiella icistia										x		BAIR
		Baridiella aff. *ronchus*			x									BAIR
		Bairdiella sp.	x		x							x		BAIR
		Ctenosciaena aff. *gracilicirrhus*	x					x						CTEN
		Ctenosciaena sp.										x		CTEN
		Cynoscion aff. *arenarius*						x						CYNO
		Cynoscion aff. *microlepidotus*	x	x										CYNO
		Cynoscion nothus						x						CYNO
		Cynoscion aff. *jamaincensis*		x										CYNO
		Cynoscion spp.	x	x				x				x		CYNO
		Equetus davidandrewi	x	x								x		EQUE
		Equetus sp.	x	x								x		EQUE

Table 3 continued

Order	Family	Species	Venezuela	Panama	Costa Rica	Dominican Republic	Cuba	Trinidad	Puerto Rico	Jamaica	Barbados	Ecuador	Brazil	ID
		Genyonemus sp.										x		GENY
		Isopisthus sp.	x	x				x				x		ISOP
		Larimus aff. *fasciatus*	x	x										LARI
		Larimus gatunensis	x	x				x						LARI
		Larimus henrii	x											LARI
		Larimus aff. *pacificus*	x											LARI
		Larimus steurbauti	x											LARI
		Larimus spp.		x	x							x		LARI
		Leiostomus sp.		x										LEIO
		Lonchurus sp.						x						LOCH
		Menticirrhus sp.		x								x		MENT
		Micropogonias ectenes										x		MICR
		Micropogonias coatesi	x											MICR
		Micropogonias furnieri	x											MICR
		Micropogonias sp.			x									MICR
		Nebris aff. *occidentalis*	x					x				x		NEBR
		Nebris sp.		x	x			x						NEBR
		Nector sp.						x						NECT
		Odontoscion dentex	x	x										ODON
		Ophioscion lundbergi	x	x				x						OPHS
		Pachypops fitchi						x						PACH
		Pachypops sp.						x						PACH
		Pachyurus junki	x											PACK
		Paralonchurus schwarzhansi	x	x										PARL
		Paralonchurus sp.										x		PARL
		Pareques sp.										x		PARQ
		Plagioscion marinus	x					x						PLAG
		Plagioscion urumacoensis	x											PLAG
		Polyclemus dumerilli			x									POLC
		Polyclemus trinidadensis		x				x						POLC
		Protosciaena neriticus	x									x		PROT
		Protosciaena sp.		x										PROT
		Seriphus sp.										x		SERI
		Sciaena bathytatos	x											SCIA
		Sciaena sp.										x		SCIA

Table 3 continued

Order	Family	Species	Venezuela	Panama	Costa Rica	Dominican Republic	Cuba	Trinidad	Puerto Rico	Jamaica	Barbados	Ecuador	Brazil	ID
		Sciaenops reyesi	x											SCOP
		Sciaenops aff. *ocellata*	x											SCOP
		Sciaenops sp.										x		SCOP
		Stellifer sp.	x	x				x				x		STEL
		Umbrina broussonetii		x										UMBR
		Umbrina aff. *canossai*	x	x	x									UMBR
		Umbrina coroides	x											UMBR
		Umbrina aff. *dorsalis*	x											UMBR
		Umbrina sp.		x								x		UMBR
		Xenotolithus sasaki						x						XENO
		Xenotolithus sp.						x						XENO
	Mullidae	*Upeneus* sp.	x											UPEN
	Percophidae	*Bembrops* sp.	x											BEMB
	Cirrhitidae	gen., sp. ind										x		CIRR
	Embiotocidae	*Cymatogaster* sp.										x		CYMA
		Hyperprosopon sp.										x		HYPER
		Micrometrus sp.										x		MICE
	Pomacentridae	*Abudefduf* sp.										x		ABUD
		Chromis sp.										x		CROM
		Pomachanthus sp.		x										PCAN
	Labridae	gen., sp. ind.										x		LABR
	Sparidae	*Diplodus oweni*			x									DIPL
		Sphaerodus paraensis											x	SPHA
		Sparus sp.			x									SPAR
		gen., sp. ind	x		x									SPAD
	Dactyloscopidae	gen., sp. ind.										x		DACT
	Gobiidae	gen., sp. ind.	x			x		x		x		x		GOBI
	Istiophoridae	*Makaira* cf. *nigricans*		x										MAKA
		cf. *Makaira* sp.	x											MAKA
	Sphyraenidae	*Sphyraena cunhai*											x	SPHA
		Sphyraena cf. *barracuda*					x							SPHA
		Sphyraena sp.	x	x	x	x		x						SPHA
	Polynemidae	*Polydactylus* sp.				x								POLC
	Trichiuridae	*Lepidopus caudatus*	x											LEPI
		Trichiurus cf. *lepturus*	x	x	x									TRIC

Table 3 continued

Order	Family	Species	Venezuela	Panama	Costa Rica	Dominican Republic	Cuba	Trinidad	Puerto Rico	Jamaica	Barbados	Ecuador	Brazil	ID
	Stromatidae	*Peprilus* cf. *medius*										x		PEPR
		Peprilus sp.	x											PEPR
Beloniformes	Belonidae	*Strongylurus* sp.										x		STRO
	Hemirhamphidae	*?Euleptorhamphus* sp.										x		EULE
		Hyporhamphus aff. *unifasciatus*	x			x				x				HYPO
		Hemirhamphus aff. *brasiliensls*				x								HEMR
		Hemirhamphus sp.										x		HEMR
Mugiliformes	Mugilidae	*Mugil* aff. *cephalus*	x	x		x				x				MUGI
		Mugil curema										x		MUGI
		Mugil sp.										x		MUGI
Pleuronectiformes	Bothidae	gen., sp. ind.										x		BOTH
	Paralichthyidae	*Citharichthys stigmaeus*										x		CITH
		Citharichthys cf. *sordinus*										x		CITH
		Citharichthys sp.	x	x				x						CITH
		Syacium sp.	x	x								x		SYAC
	Pleuronecthydae	*Ancyclopsetta* sp.		x										ANCY
		Eopsetta sp.										x		EOPS
		Isopsetta sp.										x		ISOP
	Soleidae	gen., sp. ind.										x		SOLE
	Cynoglossidae	*Cynoglossus* sp.		x										CYNG
		Symphurus sp.	x	x				x				x		SYMP
Tetraodontiformes	Diodontidae	*Diodon circumflexus*					x							DIOD
		Diodon scilae					x							DIOD
		Diodon sp.	x											DIOD

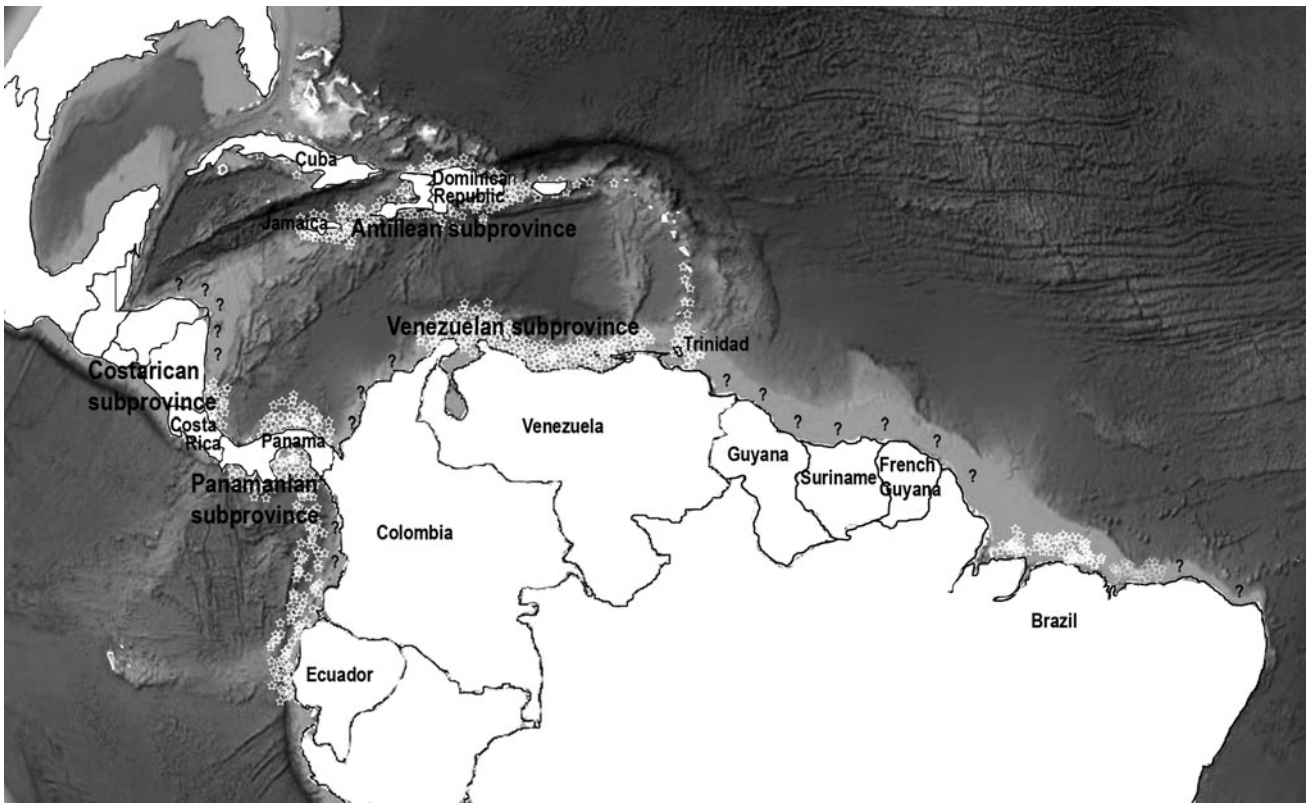

Fig. 2 The proto-Caribbean subprovinces recognized in this work (map modified from Google map). *Question marks* denote unknown fossil fish record and *star symbols* denote sedimentary deposits with potential for fossil fish occurrences

nektonic fish fauna reflects the impact of the proto-Caribbean fish fauna at the generic level in local paleoenvironment community changes in neritic, estuarine and deep water assemblages. The overall diversity remains largely the same, except for a few lamnids, such as the giant-toothed white shark and the wide-toothed mako shark.

The concept of a Gatunian Province is a valid concept in terms of the geographical and geochronological relationship with the proto-Caribbean paleofauna of invertebrate groups studied so far. In addition, we propose the Venezuelan, Antillean, Panamanian, and Costarican subprovinces as clearly recognizable assemblages of marine fishes (Fig. 2).

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